

Habitat preferences depend on substrate quality in a cooperative breeder

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Abstract

Background: The evolution of complex social organization is mediated by diverse environmental constraints, including predation risk and the availability and distribution of food resources, mating partners, and breeding habitats. The cooperatively breeding cichlid *Neolamprologus pulcher* inhabits highly distinct habitats ranging from sheer rock face to gastropod shells, rubble and sandy bottoms with dispersed stones. Physical habitat characteristics influence predator abundance and consequently the social system and reproductive performance of this species. Under natural conditions, habitat preferences should allow for optimizing the territory position within a colony.

Question: If given the choice, does *N. pulcher* distinguish between environments differing in structural complexity and the presence of sand?

Method: We created breeding groups consisting of a dominant pair and two subordinates. We manipulated structural complexity (low vs. high stone cover) and sandy environments (present vs. absent). We measured habitat preference using a four-factorial design with binary choice options.

Predictions: We predicted that groups prefer to settle in a highly structured environment providing many possibilities to hide from potential predators. We further predicted a preference for sandy bottom, especially in environments with low structural complexity, because sand allows for digging out shelters.

Results and Conclusion: *N. pulcher* favored more complex over less complex habitats, independently of the presence of sand. When fish faced low structural complexity in both experimental compartments, sand presence became a critical factor. Choosing appropriate habitats may contribute to effectively reduce predation risk.

Introduction

The availability and distribution of resources, mating partners, and suitable breeding habitats affects the social organization and mating system of many animals (Muller *et al.*, 1997; Hatchwell and Komdeur, 2000; Groenewoud *et al.*, 2016; for review see: Rubenstein and Abbot, 2017). Throughout an animal's lifespan, the choice of an appropriate habitat is crucial in order to maximize survival and reproductive success. Even within a certain habitat the microenvironment is often heterogeneous, and local resource competition might constrain life history decisions (Hamilton and May, 1977; Emlen, 1982). For example, the limited availability of high quality habitats might increase the benefits for offspring to remain philopatric (Komdeur *et al.*, 1995). Such delay in dispersal favours the formation of complex social groups and the evolution of altruistic behaviour, as observed in cooperatively breeding species where subordinate individuals help raising offspring of dominants (Koenig *et al.*, 1992; Komdeur, 1992; Komdeur *et al.*, 1995).

In many fish species, the most important habitat characteristic is the availability of protective shelters in order to avoid predation (Hixon and Beets, 1993). This leads to high levels of intra- and interspecific competition for appropriately sized shelters. Substrate breeding cichlids are among the best studied cave breeding fish species (Balshine *et al.*, 2001; Thünken *et al.*, 2007; Tanaka *et al.*, 2015; Taborsky and Wong, 2017). Within their habitats, they use a wide range of structures for hiding and breeding, extending from holes and crevices in rocks to accumulations of empty gastropod shells and shelters dug out from sand or mud (Winkelman *et al.*, 2014; Groenewoud *et al.*, 2016). Often, individuals excavate their shelters by removing sand and debris from underneath stones. The presence and extent of such movable material is of particular relevance because it allows to modulate the environment, optimizing for example the size of the shelter entrance (Dinh *et al.*, 2014; Taborsky and Wong, 2017). In contrast, in purely rocky habitats neither the number nor the size of shelters can be modified due to the lack of material that can be manipulated. Hence, the presence of sand as well as the number and size of shelters

60 influence survival and reproductive success (Balshine *et al.*, 2001; Tanaka *et al.*, 2018a). Accordingly,
61 individuals should be choosy with respect to habitat quality. Such choosiness has for example been
62 shown in the cichlid *Julidochromis transcriptus*, where females prefer spawning substrate that allow
63 them to manipulate fertilization success of males, leading to increased levels of brood care by the
64 putative fathers (Kohda *et al.*, 2009). In *Neolamprologus temporalis*, individuals generally favour rocks
65 over shells, but size dependent competition compelled smaller individuals to use a shell habitat leading
66 to restricted gene flow and potential reproductive isolation (Winkelman *et al.*, 2014).

67 In cooperatively breeding fishes, where subordinate individuals support the dominant breeders by
68 excavating cavities that serve as shelter and breeding chamber (Taborsky, 1984; Tanaka *et al.*, 2018b),
69 differences in substrate quality bear the potential to shape the social organisation of a group. For
70 example, the need for subordinates to dig out the breeding cavity is absent in populations that live on
71 purely rocky grounds (Groenewoud *et al.*, 2016). Despite these potential effects of habitat characteristics
72 on social organization and important life history decisions, experimental evidence for substrate
73 preferences is still scarce (but see: Eggleston and Lipcius, 1992; Taborsky *et al.*, 2014; Winkelman *et al.*,
74 2014). Many cooperatively breeding cichlid species appear to be specialized on habitats with limited
75 substrate variation (Tanaka *et al.*, 2015; Taborsky and Wong, 2017). In contrast, the cooperatively
76 breeding cichlid *Neolamprologus pulcher* inhabits a large variety of habitats, ranging from pure rocky
77 bottoms to sandy stretches with dispersed stones and to accumulations of empty gastropod shells
78 (Groenewoud *et al.*, 2016). *N. pulcher* is endemic to Lake Tanganyika, where it breeds in cooperative
79 groups consisting of a dominant breeding pair and 1 to 25 immature and mature subordinates (Taborsky
80 and Limberger, 1981; Heg *et al.*, 2005; Groenewoud *et al.*, 2016; Taborsky, 2016). Groups comprise a size
81 based hierarchy where smaller individuals are submissive to larger ones, including the breeding pair
82 (Taborsky, 1985, 2016). Sexes differ in their dispersal strategies, with males being more likely to disperse,
83 while females tend to queue for breeding positions in their natal group (Dierkes *et al.*, 2005; Stiver *et al.*,

2006; Hellmann *et al.*, 2016). Within a group, individuals participate in territory defence against conspecifics and other species, including space competitors and predators of eggs, young and adults (Taborsky and Limberger, 1981; Heg and Taborsky, 2010; Bruintjes and Taborsky, 2011). Furthermore, they invest in territory maintenance by removing sand underneath stones (Taborsky, 1984; Groenewoud *et al.*, 2016). These excavated cavities are of crucial importance as they serve as a hide from predators and as breeding chamber for the dominant individuals. Digging behaviour is costly in terms of energy and time invested (Grantner and Taborsky, 1998), thus individuals only invest in digging within their home territory. Indeed, digging is one way how subordinates pay to be allowed to stay in the dominant's territory (Bergmüller and Taborsky, 2005; Bergmüller *et al.*, 2005a; Zöttl *et al.*, 2013b). Territory quality, thus, influences the need of help and, as a consequence, the social system of *N. pulcher* (Balshine *et al.*, 2001; Groenewoud *et al.*, 2016). Consequently, strong preferences should occur in this species regarding where to establish a territory, which might happen either at places where a high number of suitable shelters is already present, or where the substrate would allow digging out such cavities. However, thus far habitat preferences in *N. pulcher*, and more generally in cave breeding fishes, are little understood (but see Kohda *et al.*, 2009).

The aim of this study was to elucidate habitat preferences of dominant and subordinate *N. pulcher* by providing them the opportunity to choose between habitats differing in structural complexity and in the presence of sand. We predicted that *N. pulcher* prefers (i) more complex habitats offering more shelters than less structured habitats, and (ii) sandy habitats allowing them to create shelters of their own, which should be especially important if the habitat is little structured.

Methods

Study animals

We conducted the experiment between April and May 2013 at the Ethological Station Hasli, Hinterkappelen, Switzerland. We used laboratory-reared F1 and F2 offspring of *N. pulcher* caught in the wild at the southern tip of Lake Tanganyika, near Mpulungu, Zambia. They were kept in aggregations of 5 - 30 individuals in mixed sex groups. Tanks contained 50 - 400 L of water, depending on the number of individuals. Water temperature (27 ± 1 °C) and the light:dark cycle (of 13:11 hrs) resembled natural conditions at Lake Tanganyika. The bottom of each storage tank was covered with a 2 cm sand layer and did not contain any shelters to prevent animals from breeding. Several open, semi-opaque plastic bottles at the surface served as hiding places. The fish were fed with commercial flake food five times a week, and once a week with defrosted zooplankton. In total, 80 individuals (20 groups, each containing 4 individuals) were used in the study.

Experimental set-up

We used six identical experimental tanks, each measuring 100 x 40 x 50 cm (l x b x h). Each tank was divided into two equal sized halves using an opaque grey plastic partition. The partition left a gap of 5 x 45 cm (l x h) close to the front of the tank, so that fish could switch between compartments (see Fig. 1 and 2). The water was cleaned and aerated by two biological filters, one in each compartment. Each compartment contained a different habitat, between which the focal fish could choose. In total, we used 102 stones (stone surface (mean \pm S.D.): 144.9 ± 25.8 cm²) to create four different habitats. First, we tested preferences for habitat complexity in the presence or absence of sand. Focal fish could choose between a compartment of high structural complexity equipped with 12 stones and a compartment with low structural complexity containing two stones (see Fig. 1). In half of these trials, a 2 cm layer of sand (see Fig. 1) covered the bottom of both compartments, whereas the tank was bare of sand in the other trials. Stones were spread out over the bottom of the tank, thereby creating potential shelters. Thus, we

created a habitat offering many potential shelters and a habitat offering only one shelter composed of two stones. Second, we tested preferences for sandy substrates in little and highly structured habitats. Here, one compartment contained sand and the other contained no sand, while both compartments were either equipped with 2 stones or 12 stones (see Fig. 2).

Experimental procedure

We examined four groups at the same time. One experimental run lasted 6 days. On the first day, a dominant male and a dominant female, as well as a large and a small subordinate individual, were caught from different storage tanks. Individuals of each group were unrelated and unfamiliar to each other to avoid any effects of familiarity or kinship (Le Vin *et al.*, 2010). After catching, the standard length (SL, accuracy ± 1 mm) was measured. Dominant males (mean \pm S.D.: 66 ± 5 mm) of a pair were always larger than dominant females (59 ± 5 mm). Large subordinates (33 ± 2 mm) and small subordinates (26 ± 2 mm) were considerably smaller than the dominants to lower the potential for within group conflict (Hamilton *et al.*, 2005).

At the beginning of each experimental run we placed each group into a 50 L aggregation tank for 2 days to customize the fish to each other and to ensure group stability. Each tank contained two flowerpot halves and plastic bottles close to the water surface to curb aggressive interactions. We introduced the small subordinate first, followed by the large subordinate (30 minutes later) and the dominant breeders (90 minutes later). After this group-establishing phase, the observational trials started. On the first day, all individuals of a group were placed into the experimental tank in the same way as described above. Each fish was released by hand close to the gap in the partition in the middle of the tank.

To elucidate potential changes in preferences for the different habitats over time, we observed the position of the fish three times within 24 hours. We measured the early choice by recording the location of each individual every 30 seconds for four minutes starting two hours after the release of the last fish into the experimental tank. Afterwards, the groups were kept overnight in the respective set-up tank.

The observation was continued the following morning, after 20 hours. We noted down the position of the fish every 30 seconds for 8 minutes. Here, we observed dominants and subordinates sequentially. After 23 hours, the positions of all fish were recorded again for 4 minutes every 30 seconds. Afterwards, all fish were fed and placed into a new tank containing the next set-up. The sequence of set-ups was chosen randomly, and we took care that none of the 20 groups was tested in the same sequence. After a group was removed from a tank, all stones were cleaned with water and ethanol and a new habitat was constructed in each tank to avoid preference for a particular combination of stones or side effects. During the experiment, one large subordinate and 12 small subordinates were evicted from their groups, at least during some of the trials. These fish were not allowed to be close to the bottom of the tank (Zöttl *et al.*, 2013a) and they were therefore excluded from the analyses of the respective trial.

Statistical analysis

We analysed the data in R 3.1.1 (R Core Team, 2014) using the package ‘lme4’ (Bates *et al.*, 2013). We fitted generalized linear mixed-effect models (GLMM), or linear mixed-effect models (LMM). If models were over-dispersed (Bolker *et al.*, 2009), we included an individual-based random effect (Elston *et al.*, 2001). The significance of parameters was estimated based on likelihood ratio tests (LRT), assuming a χ^2 -distribution.

In a first step, we tested for preference differences between the observation after 2h, 20h and 23h using a LMM. As the three different observations differed in time span, we calculated a preference ratio for each observation using the number of times each individual was observed in one compartment, divided by the total amount of location recordings. We applied an arcsine square root transformation in order to archive normally distributed residuals. The respective preference ratios served as response variable, and the three time points were included as a fixed factor. Additionally, we included status (dominant or subordinate) as fixed factor and tested for an interaction between status and time. Non-significant interactions were removed from the final model. To account for different experimental set-ups and

repeated measurements of the same group, we included *set-up ID* (that is the respective experimental set-up), and *group ID* (to account for the use of four individuals per group) as random effects. As there were no significant differences in preference between the 2h, 20h and 23h observation (see Results), we combined the respective measurements for further analysis, resulting in a total of 31 measurements per individual.

To answer our main question, we analysed positions within the respective set-ups. As the previous model revealed differences in the preference strength of dominants and subordinates (see Results), we continued by analysing data for dominants and subordinates independently. Therefore, we fitted two GLMMs (one for breeders, one for subordinates) for each of the four set-ups using a binomial error distribution. We used a proportional response variable including the number of times each individual was observed in each compartment. For the dominant breeder models, we included sex as factor in order to elucidate differences between males and females. For the subordinate models, we included subordinate size class as explanatory variable. We included *group ID* as random effect in all these models to account for group membership. In these models, a significant intercept indicates that preference for a certain habitat differs from chance.

Results

There was no significant difference in preference ratios between the 2h, 20h and 23h observations ($Df=2$, $\chi^2=2.017$, $p=0.36$). Overall, preferences in subordinates were less pronounced compared to breeders ($\beta=-0.17\pm0.027$, $Df=1$, $\chi^2=36.64$, $p<0.001$). These differences did not change significantly over time (time*status, $Df=1$, $\chi^2=4.49$, $p=0.11$).

Dominants and subordinates preferred the highly structured habitat over the low structured habitat, independently of whether the set-up was equipped with or without sand (see Table 1; Fig. 1: set-up 1 and 2). When keeping the structure constant in both compartments (see Fig. 2, set-up 3 and 4), the

presence of sand gained importance. If the habitats contained low structure, dominants, but not subordinates, preferred the side containing sand (see Table 1; Fig. 2 set-up 3). Finally, neither dominants nor subordinates showed significant preferences for sand when structure was high on both sides (Table 1; Fig. 2 set-up 4). The sex of the dominants and subordinate size class had no significant effect on any of our model results (see Table 1).

Discussion

Habitat characteristics are important drivers of sociality in many animals, as they can influence group size and social complexity, among other parameters (Rubenstein and Abbot, 2017). In *N. pulcher*, choosing an appropriate habitat might drastically increase predator avoidance options and, consequently, survival chances. Accordingly, individuals should prefer habitats offering protective shelters to prevent predation. We show that dominants and subordinates of *N. pulcher* prefer highly structured habitats to those with low structure, independently of the presence of sand. Indeed, focal individuals spent almost all time in the highly structured habitat (Fig. 1). This choice was made fast and consistently, as we could not detect any differences in preference between 2 h, 20 h and 23 h after start of the experiment. Additionally, there was no significant difference between dominant males and females.

While rocky habitats provide shelters that are easily accessible, shelter number and size cannot be modified. Such modification is possible in habitats containing rocks and sand. Consequently, when the structural complexity was overall low, the possibility to modify the existing shelters by removing sand gained additional importance. Under such conditions, dominants preferred sandy substrates (Fig. 2, set-up 3). The need to dig out shelters in such habitats may affect the number of group members and overall social structure (Balshine *et al.*, 2001). Indeed, a recent study showed that groups of *N. pulcher* in sandy habitats were larger (Groenewoud *et al.*, 2016). This effect was due to an increased number of

small subordinates per group, which are strongly involved in habitat maintenance, including digging and substrate cleaning (Taborsky *et al.*, 1986; Heg and Taborsky, 2010; Groenewoud *et al.*, 2016). Our results also indicate that smaller helpers tend to be more readily tolerated in the sandy compartment of a low structured habitat compared to large helpers (see Table 1; Fig. 2 set-up 3). Habitat choice has therefore the potential to influence the need for help, which can feed back on group size and group composition. However, in nature there might be trade-offs between habitat quality and other environmental factors leading to a change in habitat preferences. For example, wolf spiders (*Pardosa milvina*) show a preference for more complex over bare substrates in predator-free environments, but showed altered preferences if predator cues were given (Rypstra *et al.*, 2007). In *N. pulcher*, competition over suitable, high quality breeding sites plays an important role in shaping the social structure, as competition is directly correlated with group size, group persistence, offspring production, and antipredator behaviour (Balshine *et al.*, 2001; Heg *et al.*, 2004, 2005; Jungwirth *et al.*, 2015b). Under natural conditions, intraspecific competition leads to the differential occupation of distinct micro-habitats in *N. pulcher* and other cichlid species (Heg *et al.*, 2008; Taborsky *et al.*, 2014; Winkelmann *et al.*, 2014). Such field observations are supported by our experimental data. Preferences for the highly structured habitat providing many shelters were comparable for dominants and subordinates. This effect was different in overall less structured habitats, where subordinates were less often found on the sandy side than breeders. Such a reduced preference of subordinates compared to dominants might be explained by two non-mutually exclusive hypotheses: First, they could be the consequence of competition for access to shelters. If the structural complexity of a habitat is low, there are fewer hiding places and the space for protection is limited and not equally accessible for all individuals of a group. In the absence of predation risk, it could be advantageous for subordinates to switch to a suboptimal habitat instead of competing for access to shelters with dominants. Second, due to a lack of predation risk in combination with access to unoccupied breeding substrate subordinates might decide to disperse and occupy an own territory. Indeed, in many cooperative breeders the availability of safe breeding opportunities leads subordinate

individuals to disperse (Pruett-Jones and Lewis, 1990; Komdeur, 1992; Walters *et al.*, 1992; Tanaka *et al.*, 2016), which has also been experimentally demonstrated in *N. pulcher*, both in the laboratory and field (Bergmüller *et al.*, 2005b; Hamilton *et al.*, 2005; Jungwirth *et al.*, 2015a). Whether the weaker preferences of subordinates for a given habitat in our study were driven by high levels of aggression among group members or the possibility to safely establish own territories might be determined in futures studies.

In summary, our results reveal habitat preferences in the territorial and cooperatively breeding cichlid *N. pulcher*. They indicate that a reduction in shelter number increases the preference for sandy substrates, probably because these can be modified to increase protective potential. In populations dwelling on sand, digging by subordinates may be an important means to increase their acceptance by more dominant individuals (Zöttl *et al.*, 2013b; Quiñones *et al.*, 2016). Substrate differences therefore bear the potential to strongly influence the complex social structure of this species.

Author's contributions

DJ, MT and JGF planned the study. MT and JGF organized funding. DJ conducted the experiments and analysed the data. DJ, MT and JGF discussed the results. DJ and JGF wrote the first draft of the manuscript, which MT edited. All authors read and approved the final version of the manuscript.

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Figures

Figure 1: Preference for complex habitats

When given the choice between habitats containing few or many stones, dominants and subordinates
preferred the highly structured environment, independently of the presence (set-up 1) or absence (set-

up 2) of sand. The preference index on the y-axis depicts the number of times individuals have been observed in each compartment divided by the total counts obtained by scan sampling at 30 s intervals. Medians and interquartile ranges are shown for dominants and subordinates. Sketches on the abscissa depict the different habitats of set-up 1 and set-up 2.

Figure 2: Preference for sandy habitats

Dominants, but not subordinates, preferred sandy habitats when overall structural complexity was low (set-up 3). When habitat complexity was high, there was no significant preference (set-up 4). Preference index at the y-axis depicts the number of times individuals have been observed in each compartment divided by the total counts obtained by scan sampling at 30 s intervals. Medians and interquartile ranges are shown for dominants and subordinates. Sketches on the abscissa depict the different habitats of set-up 3 and set-up 4.

405 **Tables**

406 *Table 1:*

407 Model summaries of GLMMs showing parameter estimates of each experimental set-up for dominants
408 and subordinates, including either sex (for dominants) or size class (for subordinates). In set-up 1, the
409 compartments contained few or many rocks, with sand present in both compartments. Set-up 2 had the
410 same structure but lacked sand in both compartments. Set-up 3 contained few rocks on both sides and
411 sand in one of the compartments. Set-up 4 contained many rocks on both sides and sand in one of the
412 compartments (cf. Figures 1 and 2). Positive estimates for sex would indicate stronger preferences in
413 males compared to females and positive estimates for size class would indicate stronger preferences in
414 smaller helpers compared to larger helpers. Statistically significant effects ($p < 0.05$) are printed in bold
415 font and tendencies ($0.05 < p < 0.1$) in italics.

set-up	effects	estimate \pm SE	χ^2 -value	p-value
<i>Dominants</i>				
Set-up 1				
	Intercept	3.375 \pm 0.365		<0.001
	sex	-0.363 \pm 0.238	2.35	0.13
Set-up 2				
	Intercept	3.718 \pm 0.409		<0.001
	sex	-0.199 \pm 0.283	0.497	0.48
Set-up 3				
	Intercept	2.213 \pm 0.400		<0.001
	sex	-0.649 \pm 0.487	1.679	0.195
Set-up 4				
	Intercept	0.408 \pm 0.444		0.36
	sex	0.227 \pm 0.404	0.311	0.58
<i>Subordinates</i>				
Set-up 1				
	Intercept	3.436 \pm 0.639		<0.001
	size class	0.170 \pm 0.252	0.457	0.5
Set-up 2				
	Intercept	3.152 \pm 0.473		<0.001
	size class	0.203 \pm 0.709	0.081	0.78
Set-up 3				
	Intercept	0.440 \pm 0.302		0.15
	size class	0.685 \pm 0.400	3.038	0.08
Set-up 4				
	Intercept	-0.333 \pm 0.435		0.44
	size class	-0.324 \pm 0.703	0.209	0.65

Figure 1

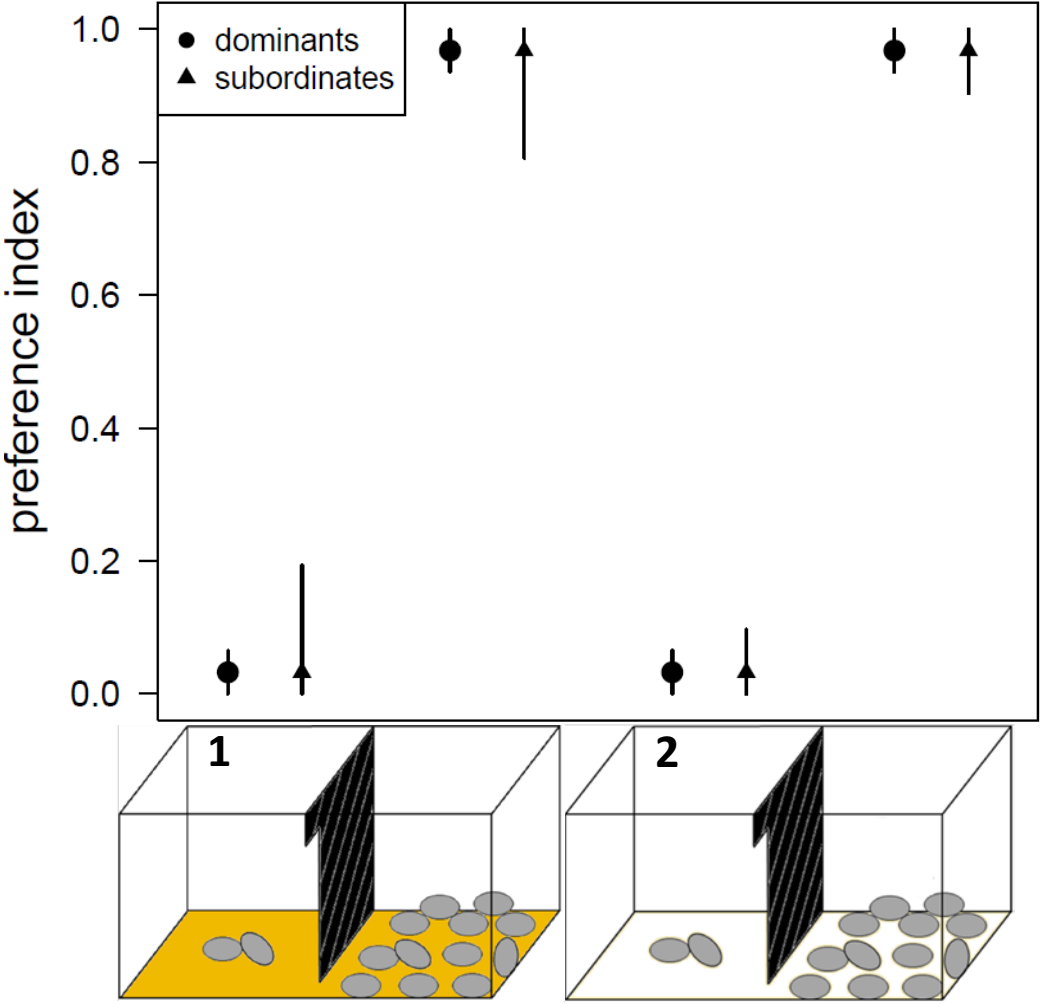


Figure 2

